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Latitudinal Differences between Palau and Yap in Coral Reproductive Synchrony[1]

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ABSTRACT: Twenty-seven species of coral were examined for reproductive activity in Palau during late spring and early summer 1993, and 10 species in Yap during the last week of May 1993. Thirteen species in Palau were gravid, and six were observed spawning during the week following May or June full moon. Spawning occurs over a minimum of 4 months in Palau. By contrast, all 10 coral species sampled in Yap, 420 km to the northeast, were well synchronized for a mass spawning event after June full moon. Intra- and interspecific spawning at equatorial latitudes is less tightly synchronized than at higher latitudes in the central Pacific. Opportunities for hybridization are a function, in part, of interspecific spawning synchrony. If hybridization serves as a mechanism for speciation in corals, then regions characterized by multispecies spawning events are more likely to serve as sites of speciation than those where spawning is more asynchronous.

IN THE PERIOD since the documentation of mass coral spawning on the Great Barrier Reef (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986), studies of coral reproduction have sought to discover the degree to which spawning synchrony occurs in other geographic regions. Additional information regarding coral reproduction exists for the Caribbean, eastern Pacific, Hawai'i, central Pacific, southern Japan, Red Sea (reviewed in Richmond and Hunter 1990), and western Australia (Simpson 1985). The degree of reproductive synchrony among species in these regions ranges from annual mass spawning, involving more than 140 species over several nights in late spring on the Great Barrier Reef, to little apparent interspecific synchrony in Hawai'i or the Red Sea. The general trend appears to be one of closer synchrony with increased annual seawater temperature range (Richmond and Hunter 1990).

Differences exist among coral species with regard to sexuality (hermaphroditic versus gonochoric), mode of reproduction (internal brooding of larvae versus broadcast spawning of gametes), and time of reproduction (Harrison and Wallace 1990). The majority of species studied to date are hermaphroditic broadcast spawners (Richmond and Hunter 1990). Most coral species have a lunar periodicity in spawning behavior that is consistent from year to year. Eggs of many coral species become pigmented (yellow, orange, or pink) several weeks before maturation and spawning (Harrison et al. 1984, Babcock et al. 1986, Heyward et al. 1987, Heyward 1988).

Despite a total of 310 coral species reported from Palau (J. Maragos, 1991, unpubl. data), fewer than a dozen species had previously been examined for reproductive activity. The most recent studies date from the early 1940s (Abe 1937, Kawaguti 1941). No published observations of coral reproduction exist for Yap. In Guam, the area closest to Palau and Yap that has been reasonably well studied, spawning behavior that results in several small-scale synchronized events has been documented over the summer months June–August (Richmond and Hunter 1990, Kenyon 1994). In this paper I present the results of monitoring selected corals for reproductive activity in Palau dur-

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ing late spring and early summer 1993, with additional observations from Yap.

MATERIALS AND METHODS

Palau

The Palau Islands are the westernmost group of the western Pacific Caroline Islands. The islands form a gently curving arc that centers around 7° N latitude and 134° E longitude. Eight different sites representing a variety of habitats were sampled, including shallow fringing reefs off volcanic and lagoonal limestone islands, upper channel slopes, and outer barrier forereefs. The maximum depth at which any coral was sampled was 9 m.

Twenty-seven species from five families were sampled and examined. Of these, 26 species are known to broadcast spawn gametes, and one (*Acropora brueggemanni* [Brook]) internally broods larvae (Atoda 1951). Twenty-four species are hermaphrodites, and three (*Porites cylindrica* [Dana], *Porites lutea* [Edwards & Haime], *Turbinaria peltata* [Esper]) are gonochoric. The genus *Acropora* was prioritized for study because its members are major components of the shallow reef assemblage and because maturing eggs are easily visible. Species were identified by reference to Veron (1993) and a list compiled by J. Maragos (1991, unpubl. data) of corals reported from Palau since 1975.

All corals sampled measured at least 30 cm in diameter, to avoid sampling young colonies that had not yet reached sexual maturity. Some species of *Acropora* are well known to propagate through asexual fragmentation (Randall 1973, Bothwell 1981, Highsmith 1982, Wallace 1985), and care was taken to minimize sampling from clonemates by choosing widely separated or morphologically distinct colonies.

Branch pieces 5–7 cm long were removed by hand, and both broken ends were examined by eye for conspicuous eggs. Collected samples were fragmented with hammer and chisel into at least five pieces, and the polyp calices along the periphery of each fragmented piece were examined with a dissecting microscope for eggs and testes. For each gravid sample, the maximum length of 10–50 eggs was measured and color of eggs was noted.

Viable portions of colonies with colored eggs were placed in a shallow flow-through tank and examined several times each evening for signs of spawning. When spawning was observed, the remaining part of the colony in the field was subsequently examined for presence or absence of gonads.

Yap

Yap Island (9° N, 138° E) is located in the western Caroline Islands, roughly 420 km northeast of Palau and 920 km southwest of Guam. Partway through the study, when it became apparent that the temporal pattern of reproduction in Palau differed from that characteristic of Guam (13° N, 144° E), a trip was made to Yap to assess the fertility of selected corals at an intermediate latitude. Two to eight colonies of each of 10 species were sampled on the shallow (3–4.5 m) reef flat adjacent to Guufnuw Channel and examined by eye for presence or absence of eggs.

RESULTS

Palau

Of 27 species examined between 6 May and 11 June 1993, 13 had gravid colonies (Table 1). Of these 13 species, 12 are known to broadcast spawn gametes, and one (*Acropora brueggemanni*) broods larvae. Of the 12 broadcast-spawning species, colonies of six species (*Acropora carduus* [Dana], *A. clathrata* [Brook], *A. florida* [Dana], *A. secale* [Studer], *Acropora* sp. [arborescent], and *Turbinaria peltata*) that were maintained in flow-through tanks were observed spawning (Table 2). Spawning by all six species occurred during the week between full moon and last quarter, between 1900 and 2200 hours. *Acropora carduus* spawned four and five nights after the May full moon. *Acropora clathrata*, *A. secale*, *A. florida*, and *Turbi-*

TABLE 1

Reproductive Status of Corals Sampled in Palau and Examined with a Dissecting Microscope for Developing Eggs or Larvae between 6 May and 11 June 1993

SPECIES	NO. OF COLONIES SAMPLED	NO. OF COLONIES GRAVID	SAMPLING INTERVAL
Acropora carduus (Dana)	6	6	6–8 May
A. hyacinthus (Dana)	10	0	6 May–2 June
A. formosa (Dana)	39	12	6 May–9 June
A. humilis (Dana)	20	0	6 May–9 June
A. nasuta (Dana)	17	0	6 May–9 June
A. tenuis (Dana)	22	0	6 May–9 June
A. echinata (Dana)	18	0	6 May–9 June
A. digitifera (Dana)	24	0	6 May–9 June
A. secale (Studer)	12	2	6 May–11 June
A. divaricata (Dana)	2	2	8 May
A. pulchra (Brook)	4	0	8–16 May
A. cytherea (Dana)	13	0	8 May–2 June
A. austera (Dana)	5	0	8 May–2 June
A. granulosa (Edwards & Haime)	5	5	8 May–8 June
A. clathrata (Brook)	16	16	8 May–11 June
A. florida (Dana)	19	15	8 May–11 June
A. valenciennesi (Edwards & Haime)	4	1	12–24 May
A. horrida (Dana)	4	4	14 May–10 June
A. paniculata (Verrill)	1	1	4–11 June
Acropora sp. (arborescent)	2	2	4–11 June
A. brueggemanni (Brook)	12	8	6–22 May
Porites lutea (Edwards & Haime)	3	0	6 May
Porites cylindrica (Dana)	8	0	6–8 May
Echinopora lamellosa (Esper)	5	0	6–22 May
Montipora aequituberculata (Bernard)	13	0	8–22 May
Turbinaria peltata (Esper)	1	1	21 May–11 June
Pectinia paeonia (Dana)	4	0	22 May

TABLE 2

Summary of 1993 Spawning Dates and Egg Size for 10 Fertile Coral Species in Palau

SPECIES	SPAWNING DATES	MEAN DIAMETER SPAWNED EGGS (μm)	MEAN DIAMETER WHITE EGGS (μm)
Acropora carduus	10, 11 May (4, 5)	531	—
A. formosa	—	—	470
A. secale	11 June (6)	NR	674
A. granulosa[a]	?June?	(698)	540
A. clathrata	11 June (6)	566	—
A. florida	11 June (6)	562	—
A. horrida	—	—	567
A. paniculata	—	—	610
Acropora sp. (arborescent)	12 June (7)	NR	555
Turbinaria peltata	11 June (6)	643	—

Note: Numbers in parentheses following spawning dates refer to number of nights after the full moon. Sizes of immature, white eggs were measured shortly after the June full moon. Between 30 and 150 eggs were measured for each species. NR, not recorded.
[a]Though not observed, spawning probably occurred in colonies with darkly pigmented eggs.

naria peltata spawned six nights after the June full moon, and *Acropora* sp. (arborescent) spawned one night later. Subsequent observations of gravid colonies that had been flagged for relocation on the reef confirmed that spawning had occurred in these colonies as well.

Seven of the 13 gravid species (*Acropora florida*, *A. secale*, *Acropora* sp. [arborescent], *A. granulosa* [Edwards & Haime], *A. formosa* [Dana], *A. horrida* [Dana], *A. paniculata* [Verrill]) still had immature white eggs at the end of the study period (11 June). Of these, three species had some colonies that had spawned after the 4 June full moon (*Acropora florida*, *A. secale*, *Acropora* sp. [arborescent]). The size of eggs still developing in gravid colonies of these species (Table 2) suggests that spawning probably also occurred in July.

Although spawning was not documented in *A. granulosa*, the presence of colonies with either darkly pigmented or white eggs shortly after the June full moon suggests that spawning is probably "split" over at least 2 months for this species as well. The size of developing eggs in *A. formosa*, *A. horrida*, and *A. paniculata* when last sampled around June full moon (Table 2) suggests that maturation and spawning occurred in July, although continued development into August cannot be ruled out. Developing eggs in *A. divaricata* (Dana), *A. valenciennesi* (Edwards & Haime), and *A. brueggemanni* were not monitored long enough to determine time of maturation and release (Table 1).

The degree of intraspecific synchrony varied greatly among species and sites. All examined colonies of *A. carduus*, *A. horrida*, *A. clathrata*, and *A. granulosa* were gravid when first sampled (Table 1). By contrast, even at the same study site some colonies of *A. florida*, *A. secale*, and *A. brueggemanni* were gravid while others were not. Some species when sampled from different sites showed similar degrees of reproductive development, but other species showed disparities. For example, ripe colonies of *A. clathrata* were found on both the east and west barrier reef slope (Lighthouse Channel and Ulong Channel area, respectively). By contrast, the fertility of colonies of *A. formosa* varied between study sites. Either all the colonies of this species examined from a given site were gravid (fringing reefs off Malakal Island and a site in the Rock Islands) or all were not gravid (e.g., off Ulong Island and the K-B Bridge).

Yap

Of 10 species examined, all had colonies with darkly pigmented eggs (Table 3). Every colony of every species examined had conspicuous eggs. Two species (*A. danai* and *A. formosa*) had some colonies with colored, ripe eggs, but other colonies had immature white eggs. No colony had eggs in both developmental stages. All sampled colonies of

TABLE 3

SUMMARY OF CORALS SAMPLED AND EXAMINED WITH THE NAKED EYE FOR DEVELOPING EGGS ON THE REEF FLAT ADJACENT TO GUUFNUW CHANNEL, YAP, ON 27 MAY 1993, 8 DAYS BEFORE THE 4 JUNE FULL MOON

SPECIES	NO. OF COLONIES SAMPLED	NO. OF COLONIES WITH COLORED EGGS	NO. OF COLONIES WITH WHITE EGGS
Acropora danai	8	6	2
A. formosa	6	3	3
A. valida	6	6	0
A. digitifera	3	3	0
A. tenuis	3	3	0
A. cytherea	6	6	0
A. hyacinthus	6	6	0
A. florida	6	6	0
A. surculosa	2	2	0
Montipora digitata	4	4	0

the remaining eight species had colored, ripe eggs.

DISCUSSION

Lunar Periodicity and Tidal Regime

The six coral species that were observed spawning in Palau all did so between full moon and lunar last quarter. These observations are in agreement with studies from other regions, including the Great Barrier Reef, Okinawa, and Guam (Richmond and Hunter 1990, Kenyon 1994).

On any given spawning night, the time of spawning occurred roughly midway between low and high tide, a period of maximum incoming tidal current flow. Such timing may serve to facilitate mixing of gametes and dispersal of developing embryos.

Intraspecific Synchrony

During spawning, all or most of the mature reproductive products of a colony are expelled (Wallace 1985, Kenyon 1992). On the Great Barrier Reef, where spawning at a given site is highly synchronized during a major annual event, some *Acropora* species may spawn over two or more periods, as suggested by the presence of two categories of egg size in dissected samples (Wallace 1985). Degeneration or resorption of unspawned eggs has not been documented in *Acropora*.

Gravid corals sampled in Palau showed substantial variation in intraspecific synchrony, but those in Yap were well synchronized. The degree of intraspecific synchrony may be characteristic of a particular species. For example, spawning in *A. danai* in Guam typically occurs in two consecutive summer months (pers. obs.). The presence of colonies with either white or colored eggs suggests that the same is true for this species in Yap (Table 3). Similarly, *A. formosa* in Yap probably demonstrates "split" spawning, because some colonies had ripe eggs shortly before June full moon while others contained immature white eggs. Variability in egg size among gravid colonies of *A. formosa* in Palau suggests that spawning may occur in both July and August.

Interspecific Synchrony

Substantial interspecific synchrony has been documented among corals on the Great Barrier Reef and, to a lesser extent, in Okinawa and Guam (Heyward et al. 1987, Richmond and Hunter 1990). The presence of colored eggs in nearly every colony of 10 species examined in Yap 1 week before the June full moon suggests that a major spawning event occurred in those waters shortly thereafter. Local residents are aware of the mass synchronous spawning of corals from four to eight nights after the full moon just before the wet season (B. Goldman, pers. comm.). By contrast, the pattern in Palau indicated by this study is one of greater asynchrony. The gravid corals identified during this study were spread out over at least several months in their spawning periodicity. Spawning was directly observed in May (*A. carduus*) and June (*A. clathrata*, *A. secale*, *A. florida*, *Acropora* sp. [arborescent], *Turbinaria peltata*) while other species still had immature eggs developing (*A. formosa*, *A. horrida*, *A. paniculata*, *A. granulosa*). The size of developing eggs in these species (Table 2) suggests that spawning probably occurred in July and possibly in August. Some species clearly spawn over at least 2 months (e.g., *A. florida*, *A. secale*, *Acropora* sp. [arborescent]).

In addition, a number of species that are important components of the shallow reef assemblage, and that participate in synchronized multispecies spawnings elsewhere, were devoid of gonads at the commencement of this study (*A. digitifera* [Dana], *A. humilis* [Dana], *A. tenuis* [Dana], *A. echinata* [Dana], *A. nasuta* [Dana], *A. cytherea* [Dana], and others [see Table 1]). There is currently no evidence to choose among several alternatives describing their reproductive behavior in Palau: (1) these and other species are well synchronized, releasing gametes earlier in the year, (2) these and other species are asynchronous, with spawning spread out over several months, or (3) these and other species are sterile. Only future research will discriminate among these alternatives. Even given the most conservative premise of synchronous spawning by these species in April, the time range of coral reproduction in Palau would be a minimum of 4 months, from April to July.

The study reported here lends weight to the trend noted by Richmond and Hunter (1990) that reproductive seasonality and synchrony diminish at lower latitudes (Oliver et al. 1989), accompanied by decreased temperature range (Shlesinger and Loya 1985, Babcock et al. 1986). In Palau the seawater temperature is stable year-round, ranging between 28 and 31° C, with an average of around 29° C (Hatai 1937). In this regard it is interesting to note that giant clams (*Tridacna* and *Hippopus* spp.) in Palau have been found in spawning condition throughout the year, whereas in more seasonal climates of Australia and Fiji spawning is more likely to occur in the warmer summer months (Heslinga et al. 1990).

Biogeographical Implications of Reproductive Synchrony

The center of high coral diversity lies within the triangle demarcated by the northern Philippines, Borneo, and Papua New Guinea and extends along a line south to the southern Great Barrier Reef (Stehli and Wells 1971, Veron 1985, 1993). Coral biogeographers have long debated whether the Indo-Pacific center of high diversity is a "cradle" in which species have arisen (Stehli and Wells 1971, Potts 1984, McManus 1985) or a "museum" in which species have accumulated (Heck and McCoy 1978, Rosen 1984, Jokiel 1990, Wallace et al. 1991).

Considerations of the degree of spawning synchrony and the opportunities for hybridization suggest a new approach to this persistent problem. Recent experimental work in Australia (Willis et al. 1992, Kenyon 1994), Okinawa, Guam (R. Richmond, pers. comm.), and Palau (Kenyon 1994) has demonstrated that hybridization can occur between species and even between genera during synchronized multispecies spawning events. In other animal and plant groups where hybridization has been studied, it can result in the production of hybrid swarms (Palmer 1948, Tucker 1952, Sibley 1954, Grant 1981, Wilde and Echelle 1992), introgression (Anderson 1949, Turner 1971, Arnold 1992), or hybrid speciation (Grant 1981, Arnold et al. 1990, Riesenberg et al. 1990, DeMarais et al. 1992). If hybridization operates as a mechanism of speciation in corals, then the degree to which coral spawning is synchronized between species influences the opportunities for hybridization and therefore the biogeography of speciation. Hybridization is in part a function of spawning synchrony. Geographic regions with high species diversity and multispecies spawning, such as the Great Barrier Reef, provide more opportunities for hybridization than regions with lower species diversity and greater asynchrony of spawning, such as the Red Sea (Shlesinger and Loya 1985) or Hawai'i (Heyward 1985, Hunter 1989, Kenyon 1992). Aside from two sites on the northern coast of Papua New Guinea (Oliver et al. 1989), no other published data exist regarding temporal patterns of coral reproduction in the high-diversity triangle demarcated by Indonesia, Borneo, and Papua New Guinea. The total of 69 genera presently documented in Palau is comparable with the generic totals for the Great Barrier Reef and places Palau within the high coral diversity center of the Indo-Pacific (J. Maragos, 1991, unpubl. data). To the extent that hybridization in corals may operate as a mechanism for speciation, the trend toward spawning asynchrony in both Palau and northern Papua New Guinea supports the view that the high-diversity triangle represents a process of species accumulation more than a process of species origin.

In contrast, the most recent species inventory in Yap (A. Orcutt, 1989, unpubl. data) documents 102 fewer species and 12 fewer genera than are present in Palau. Despite the fewer number of species in Yap, the high degree of reproductive synchrony that is documented in the study reported here implies that there are many opportunities for hybridization. Coral populations in equatorial latitudes, as exemplified by Papua New Guinea and Palau, may be less likely to function as sites of hybrid-driven speciation than those in higher-latitude regions such as Yap, Guam, and Australia, which are characterized by more highly synchronized interspecific spawning.

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LITERATURE CITED

ABE, N. 1937. Postlarval development of the coral *Fungia actiniformis* var. *palawensis* Doderlein. Palao Trop. Biol. Stn. Stud. 1: 73–93.

ANDERSON, E. 1949. Introgressive hybridization. Wiley, New York.

ARNOLD, M. L. 1992. Natural hybridization as an evolutionary process. Annu. Rev. Ecol. Syst. 23:237–261.

ARNOLD, M. L., J. L. HAMRICK, and B. D. BENNETT. 1990. Allozyme variation in Louisiana irises: A test for introgression and hybrid speciation. Heredity 65:297–306.

ATODA, K. 1951. The larvae and postlarval development of some reef-building corals. III. *Acropora brueggemanni* (Brook). J. Morphol. 89:1–13.

BABCOCK, R. C., G. D. BULL, P. L. HARRISON, A. J. HEYWARD, J. K. OLIVER, C. C. WALLACE, and B. L. WILLIS. 1986. Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. (Berl.) 90:379–394.

BOTHWELL, A. M. 1981. Fragmentation, a means of asexual reproduction and dispersal in the coral genus *Acropora*—a preliminary report. Pages 137–144 *in* Proc. 4th Int. Coral Reef Symp., Manila.

DEMARAIS, B. D., T. E. DOWLING, M. E. DOUGLAS, W. L. MINCKLEY, and P. C. MARSH. 1992. Hybrid origin of *Gila seminuda* (Pisces: Cyprinidae): Implications for evolution and conservation. Proc. Natl. Acad. Sci. U.S.A. 89:2747–2751.

GRANT, V. 1981. Plant speciation. Columbia University Press, New York.

HARRISON, P. L., and C. C. WALLACE. 1990. Reproduction, dispersal and recruitment of scleractinian corals. Pages 133–207 *in* Z. Dubinsky, ed. Coral reefs: Ecosystems of the world.

HARRISON, P. L., R. C. BABCOCK, G. D. BULL, J. K. OLIVER, C. C. WALLACE, and B. L. WILLIS. 1984. Mass spawning in tropical reef corals. Science (Washington, D.C.) 223:1186–1189.

HATAI, S. 1937. The Palao Tropical Biological Station. Palao Trop. Biol. Stn. Stud. 1:1–15.

HECK, K. L., JR., and E. D. MCCOY. 1978. Long-distance dispersal and the reef-building corals of the eastern Pacific. Mar. Biol. (Berl.) 48:349–356.

HESLINGA, G. A., T. D. WATSON, and T. ISAMU. 1990. Giant clam farming. Pacific Fisheries Development Foundation (NMFS/NOAA), Honolulu, Hawai'i.

HEYWARD, A. J. 1985. Sexual reproduction in five species of the coral *Montipora.* Tech. Rep. Hawai'i Inst. Mar. Biol. 37:170–178.

———. 1988. Reproductive status of some Guam corals. Micronesica 21:272–274.

HEYWARD, A. J., K. YAMAZATO, T. YEMIN, and M. MINEI. 1987. Sexual reproduction of corals in Okinawa. Galaxea 6:331–343.

HIGHSMITH, R. C. 1982. Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7:207–226.

HUNTER, C. L. 1989. Environmental cues

controlling spawning in two Hawaiian corals: *Montipora verrucosa* and *M. dilitata.* Proc. 6th Int. Coral Reef Symp., Townsville 2:727–732.

JOKIEL, P. L. 1990. Transport of reef corals into the Great Barrier Reef. Nature (Lond.) 347:665–667.

KAWAGUTI, S. 1941. On the physiology of reef corals. V. Tropisms of coral planulae considered as a factor of distribution on the reef. Palao Trop. Biol. Stn. Stud. 2: 319–328.

KENYON, J. C. 1992. Sexual reproduction in Hawaiian *Acropora*. Coral Reefs 11:37–43.

———. 1994. Hybridization and polyploidy in the coral genus *Acropora.* Ph.D. dissertation, University of Hawai'i at Mānoa, Honolulu.

MCMANUS, J. W. 1985. Marine speciation, tectonics and sea-level changes in Southeast Asia. Proc. 5th Int. Coral Reef Congr., Tahiti 4:133–138.

OLIVER, J. K., R. C. BABCOCK, P. L. HARRISON, and B. L. WILLIS. 1989. The geographic extent of mass coral spawning: Clues to proximate and ultimate causal factors. Proc. 6th Int. Coral Reef Symp., Townsville 2:803–810.

PALMER, E. J. 1948. Hybrid oaks of North America. J. Arnold Arbor. Harv. Univ. 29:1–48.

POTTS, D. C. 1984. Generation times and the Quaternary evolution of reef-building corals. Paleobiology 10:48–58.

RANDALL, R. H. 1973. Reef physiology and distribution of corals at Tumon Bay, Guam, before crown-of-thorns starfish *Acanthaster planci* (L.) predation. Micronesica 9:119–158.

RICHMOND, R. H., and C. L. HUNTER. 1990. Reproduction and recruitment of corals: Comparisons among the Caribbean, the tropical Pacific, and the Red Sea. Mar. Ecol. Prog. Ser. 60:185–203.

RIESENBERG, L. H., R. CARTER, and S. ZONA. 1990. Molecular tests of the hypothesized hybrid origin of two diploid *Helianthus* species (Asteraceae). Evolution 44:1498–1511.

ROSEN, B. R. 1984. Reef coral biogeography and climate through the late Cainozoic: Just islands in the sun or a critical pattern of islands? Pages 201–262 *in* P. Brenchley, ed. Fossils and climate. Wiley, New York.

SHLESINGER, Y., and Y. LOYA. 1985. Coral community reproductive patterns: Red Sea versus the Great Barrier Reef. Science (Washington, D.C.) 228:1333–1335.

SIBLEY, C. G. 1954. Hybridization in the red-eyed towhees of Mexico. Evolution 8: 252–290.

SIMPSON, C. J. 1985. Mass spawning of scleractinian corals in the Dampier Archipelago and the implications for management of coral reefs in Western Australia. West. Aust. Dep. Conserv. Environ. Bull. 244: 1–35.

STEHLI, F. G., and J. W. WELLS. 1971. Di versity and age patterns in hermatypic corals. Syst. Zool. 20:115–126.

TUCKER, J. M. 1952. Evolution of the California oak *Quercus alvordiana.* Evolution 6:162–180.

TURNER, J. R. G. 1971. Two thousand generations of hybridization in a *Heliconius* butterfly. Evolution 25:471–482.

VERON, J. E. N. 1985. Aspects of the biogeography of hermatypic corals. Proc. 5th Int. Coral Reef Congr., Tahiti 2:83–88.

———. 1993. Corals of Australia and the Indo-Pacific. University of Hawai'i Press, Honolulu.

WALLACE, C. C. 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora.* Mar. Biol. (Berl.) 88:217–233.

WALLACE, C. C., J. M. PANDOLFI, A. YOUNG, and J. WOLSTENHOLME. 1991. Indo-Pacific coral biogeography: A case study from the *Acropora selago* group. Aust. Syst. Bot. 4: 199–210.

WILDE, G. R., and A. A. ECHELLE. 1992. Genetic status of pecos pupfish populations after establishment of a hybrid swarm involving an introduced congener. Trans. Am. Fish. Soc. 121(3): 277–286.

WILLIS, B. L., R. C. BABCOCK, P. L. HARRISON, and J. K. OLIVER. 1985. Patterns in the mass spawning of corals on the Great

Barrier Reef from 1981 to 1984. Proc. 5th Int. Coral Reef Congr., Tahiti 4: 343–348.
WILLIS, B. L., R. C. BABCOCK, P. L. HARRISON, and C. C. WALLACE. 1992. Experimental evidence of hybridization in reef corals involved in mass spawning events (abstract). Proc. 7th Int. Coral Reef Symp., Guam 1: 504.